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Differences in Herbivore Performance Between a Wild Population and a Laboratory Population of Western Spruce Budworm

(Short Title: Differences in Herbivore Performance)

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Differences in Herbivore Performance Between a Wild Population and a Laboratory Population of Western Spruce Budworm

ABSTRACT

1. Wild and lab-reared populations of western spruce budworm, Choristoneura occidentalis Freeman, were used to examine whether differences exist between them in terms of survival, mass, and fecundity.
2. There is no difference in hatch success between lab and wild populations of budworm or between laboratory budworm placed in the field either early or later in the season. The treatment of "late lab" meant that lab-reared larvae were placed on more mature foliage.
3. Results from hatch success of egg masses and of number of larvae that emerge from egg masses suggest that there is no difference in the fecundity of the two populations; the population fitness and population growth over time will be the same for lab and for wild budworm populations.
4. There were no differences in pupal survival rates from either population. Therefore, the amount of adults that will contribute to the next generation are equivalent among treatments (wild, lab, late lab). Results indicate that there are differences in pupal mass between treatments. However, the differences between treatments amounted to only 11-16 percent; we believe that the slight differences in mass is not affecting the overall population dynamics of budworm.

5. Tree age may have an effect on the fitness of budworm populations. However, tree age cannot be the only factor to affect budworm populations. Other work suggests that host foliar chemistry constitutes a significant portion of the variance explaining the relationship between budworm herbivory/fecundity and extrinsic factors.

KEY WORDS

Western Spruce budworm, Choristoneura occidentalis, performance, population dynamics, survival, fecundity.

INTRODUCTION

The question of whether field studies performed on lab-reared insects are biologically relevant is of interest to many scientists. Debate can be issued forth by other researchers because of the use of laboratory organisms, with critical reviewers proclaiming that lab-reared insects under "ideal" environmental conditions do not represent the natural population, and that results obtained from these organisms do not have any predictive power.

While these arguments are valid in some, if not many cases, experiments can be conducted to determine just how different laboratory organisms are from wild organisms. Results from such experiments can support or refute arguments that laboratory organisms are biologically relevant to represent the true, natural population. Ecologists often become interested, not only in nature, but in laboratory systems and mathematical models; these have and will continue to play a critical role in ecological development. However, "...it is the real world that we are interested in, and the worth of models and simple laboratory experiments must always be judged in terms of the light they throw on the working of more natural systems....A major aim of science is to simplify, and thereby make it easier to understand the complexity of the real world" (Begon et al. 1986, introduction).

In this study, we set out to determine how realistic it is to use lab-reared budworms to make predictions about the natural

population. We wanted to determine if there were differences in hatch success, pupal survival, and pupal mass between wild, lab, and late lab treatments. Also, we wanted to determine if the age of the host tree affected pupal mass between males and females.

If there are no differences between wild populations and lab populations, the ability to use laboratory insects to make predictions about natural populations is a valuable tool to researchers. The work that has been done so far on the Western Spruce budworm can be considered valid in making management decisions concerning outbreak populations. It also allows work to be done throughout the year instead of waiting for field seasons. This has strong implications for pest species, since the faster one can learn about the insects' population dynamics, the sooner effective management plans can be implemented.

Natural History

The Western Spruce budworm (WSBW), Choristoneura occidentalis (Lepidoptera: Tortricidae), is a major defoliator of coniferous trees in the Western United States and Canada (Brookes et al. 1987). Its principal hosts are Douglas-fir (Pseudotsuga menziesii), White fir (Abies concolor), and Englemann spruce (Picea englemannii). During intense budworm outbreaks, damage to individual trees, as well as whole forest stands can be severe, often fatal. Stand damage history is known to have an effect on budworm densities (Fleming et al. 1983). Some trees are more susceptible to budworm attack while others

are more resistant (Clancy et al. 1993).

The Western Spruce budworm exhibits five distinct phases in one life cycle: egg, early larval, late larval, pupal, and adult (moth). Eggs are laid in late July and August, and hatch out within ten days. First instar larvae do not feed, but occasionally will eat their egg cases. Without feeding on foliage, first instars will molt into second instars, and it is during this phase that they enter diapause. At the arrival of spring, second instar larvae emerge from diapause and start feeding on buds or fresh, new foliage. Larvae pass through four more instars before pupating in late June/early July. The pupal stage lasts for five to eight days, upon which a moth will eclose. Adult moths will mate typically within 24 hours upon emergence and eggs will be laid three to seven days later, completing the cycle.

Study Site

The site that we chose to work at, Little Springs, is located on the San Francisco Mountains in the Coconino National Forest, 10 miles north of Flagstaff, Arizona. This site is one of the few areas populated by the Western Spruce budworm in Northern Arizona and it is the most recently reported population not yet reaching outbreak proportions. This site is composed mainly of Douglas-fir.

METHODS

Comparison of Lab and Wild Budworms

Thirty-six Douglas fir trees at Little Springs were randomly chosen and marked, using numbered tags. Three equal sized branches from each tree were haphazardly chosen for removal of budworms. Lower branches were used due to their accessibility. Once three branches on each tree were cleared of any naturally occurring budworms, one branch received five wild budworm larvae, the second branch received five lab-reared budworm larvae, and the third branch received five lab-reared budworm larvae placed later in the season, when foliage was more mature. The branches were immediately bagged, using fine mesh bags, to keep out any wild budworms and to keep the five in the bag from escaping.

Larvae were kept in the bagged branches in the field until, upon visual inspection, fifty percent of the larvae had pupated. Then, the branches were cut, brought back to the lab, and processed within 24 hours. The laboratory maintained conditions ideal for budworm development (Clancy 1991). Records were kept of the tree number, bag type, number of larvae and pupae collected, and pupal mass. Larvae were placed in labelled petri dishes with fresh foliage to allow for continued development into pupae. Pupae collected from bags and petri dishes were sexed and placed in labelled trays. The trays were left in the refrigerator until they were filled (24 pupae/tray).

Once one female and one male tray was filled with the same

type (wild, lab, or late lab), the 48 pupae were placed in a brown paper mating bag with suitable Douglas-fir foliage for oviposition, and allowed to eclose. Moths were allowed to mate for seven days, and then transferred to another similar mating bag. The egg masses from the first mating bag were collected, placed in individual shell vials, and labelled. This was done with egg masses from the second mating bag in the same manner.

Most egg masses hatched within ten days. However, unhatched egg masses were allowed three weeks to hatch. After three weeks, any unhatched eggs were assumed to be inviable. Measurements of hatched and total lengths and widths of egg masses and the number of eggs and larvae emerged were recorded.

Host Characteristics

Measurements of DBH (diameter at breast height), tree height, and tree age were taken on each of our marked trees. Tree height was recorded to the nearest 0.5 meter. Tree age was determined by counting the growth rings from a core taken at breast height. On our youngest trees, a core was not taken, for fear of causing tree mortality. The tree age was estimated by growth whorls on the stem. These measurements were taken once all bags were removed, so that the effects of coring a tree would not affect the budworms in any way.

RESULTS

The distribution of the number of eggs in F_1 egg masses

approximates a normal distribution, although the peak is slightly skewed to the left (Figure 1). The distribution of the number of larvae hatched from F_1 egg masses also approximates a normal distribution, with an even better fit (Figure 2). However, in light of this, our sample sizes are large enough to assume that the samples were taken from a population with a normal distribution, so that parametric tests (e.g., ANOVAs, t-tests) can be run on these data sets.

Comparison of Lab and Wild Budworms

There is no difference in hatch success between lab and wild populations of budworm (Figure 3, $p > 0.5$). The percentage of eggs that hatched, for both treatment groups, was near eighty percent. This percentage is high enough to sustain a large mortality rate over winter and still produce large numbers of budworms in the spring (Miller 1958, Brookes et al. 1987).

There is no difference in hatch success between lab-reared larvae placed on Douglas-fir foliage either early or late in the season (Figure 4, $p > 0.3$). Again, the percentage of eggs that hatched, for both treatment groups, was over eighty percent. The level of maturity of Douglas-fir foliage does not seem to be important in the hatch success of larvae from egg masses.

There also is no difference in the number of larvae that emerged from F_1 egg masses between lab-reared and wild budworm (Table 1, $F = 0.125$, $p < 0.728$). There is more variation between groups than among groups, stating that, while there is

considerable variation in the number of larvae that emerge (i.e., depending on the size of the egg mass), the overall variation among groups is not different.

Survival Rates

Figure 5 shows the survival rates of pupae from each of the treatment groups. The data show that there are no significant differences in survival rates between females and males and also between treatments (Figure 5, $p > 0.1$). Whether a budworm is from a wild, natural population or from a lab-reared, non-diapausing population makes no difference in the number of pupae that emerge from pupal cases.

Pupal Mass

Pupal mass is affected by sex and by treatment (Figure 6). Pupal masses are significantly different between males and females ($t_s = 145.33$, $p < 0.0001$; also see Figure 6). It is well known from the literature that female insects are generally heavier than male insects of the same species (e.g., Gwynne 1984, Clancy 1991, Ochieng'-Odero 1991, 1992). However, pupal mass decreases by treatment in the fashion wild > lab > late lab (Figure 6, $p < 0.05$). Although wild pupae are heavier than lab-reared pupae, the difference is only a matter of 11-16 percent. This may not be a critical difference to affect fecundity.

Figure 7 shows pupal weights in relation to tree age, separated by sex. The solid circles represent females and the

open squares represent males. From the figure, one can see that the distribution of female pupal weights by tree age shows no consistent pattern (Figure 7, $r^2 = 0.46$, $p > 0.05$). However, the distribution of male pupal weights by tree age shows a more consistent pattern, conforming to a best fit line (Figure 7, $r^2 = 0.67$, $p < 0.01$).

DISCUSSION

Many laboratory studies are conducted on insects, mainly due to their simplicity. Laboratory experiments are easier to control, manipulate, and to eliminate confounding variables that may be difficult to do in the field. Laboratory studies on non-diapausing insects can be conducted throughout the year, eliminating the break in productivity that occurs in areas with seasonal climates, where field seasons are restricted to a couple of months. Therefore, if wild and lab populations can be shown to have no differences in performance, results from laboratory insects represent a sample from the natural population.

Figures 3-4 show that there are no differences in survival of eggs or larvae between wild and lab and between lab and late lab budworms. While there are individual egg mass differences due to variations in the size of egg masses, the variation within each group far outweighed the variation among groups (personal observation). Just based on egg masses, having no differences in hatch success of eggs can be correlated to the number of budworms that will survive for each population. This also can be

correlated to the fecundity of the females from each population. The amount of successful progeny that each female moth leaves directly relates to the fitness of that individual. Therefore, the fitness of the two populations (i.e., three treatments) are equal.

Another result that suggests that the fitness of each population is equal is shown in Table 1. This table compares the mean number of larvae emerged from egg masses between lab and wild budworms. Here, it is shown that the number of larvae from each population is not different. Again, there is considerable variation within groups due to a large variation in egg mass areas, but a small variation between groups. Therefore, we can conclude that the population fitness and population growth over time will be the same for each treatment.

Pupal survival rates also show that there is no difference between the three treatments (Figure 5). The graph represents the amount of pupae that emerged into adults. Therefore, the amount of adults (and thus, reproductive females) that will contribute to the next generation are equivalent among treatments, suggesting no viable differences between them.

Pupal mass was also compared between sexes and between treatments (Figure 6). Not surprisingly, there is a significant difference between females and males ($p < 0.0001$); this type of result is well documented in the literature (e.g., Gywnne 1984, Clancy 1991, Ochieng'-Odero 1991, 1992). There were significant differences among treatments ($p < 0.05$), but these differences

only amounted to 11-16 percent of the total pupal mass. While this difference was detectable, how relevant this difference is may be questionable. A difference of 11-16 percent in body mass may not affect fecundity. Our previous data show that there are no differences in pupal survival, in egg mass viability, or in number of larvae between populations. Therefore, this slight difference in mass is not affecting the overall population dynamics of either wild or lab budworms.

Since we cannot find evidence of differences in performance between lab and wild budworms, we wanted to determine if there were any extrinsic factors affecting the population of budworms. One possible factor influencing the population dynamics of budworms is tree age. Figure 7 shows results from a best-fit regression of pupal mass by tree age. There is no consistent pattern of the distribution of female pupal mass. Since female pupal mass is strongly correlated with potential fecundity (Wagner et al. 1987), this implies that there may not be much effect of tree age on the growth of budworm populations. In contrast, the regression suggests that male pupal mass may be affected by the age of the host tree. However, the slope only explains 67 percent of the variation around the regression line; there is still 33 percent unexplained variance to account for. Quite possibly, tree age has an effect on both male and female pupal mass, but tree age cannot be the only factor contributing to the population dynamics of budworms. There are other factors that may be involved.

Work by Clancy and others (1988, 1992, 1993) have shown that foliar chemistry of the host plays an important part in budworm herbivory and fecundity. Clancy et al. (1988) have shown that the concentrations and balances of nitrogen and minerals in current year foliage among host species are different, and that these variations are important in determining budworm performance. It was also shown (Clancy 1992) that low levels of sucrose and nitrogen provide a "better host" to developing budworm larvae than foliage containing concentrations of these at the higher end of the host's spectrum. Clancy also hypothesizes that these variations may be the basis of determining resistence in Douglas-fir hosts (Clancy 1992). This hypothesis was supported by further work (Clancy et al. 1993). "Resistent trees may suffer low defoliation because they provide a food source that is poorly matched to the budworm's nutritional requirements with respect to concentrations of sugars and balances of key minerals to N" (Clancy 1991).

From previous work, it has been shown that other factors, besides tree age, have an affect on budworm survival and fecundity. While the population dynamics of the Western Spruce budworm are not completely understood, much more progress can be made by researchers on Choristoneura occidentalis since this study has shown that there are no significant differences between wild populations and laboratory-reared populations. The non-diapausing, laboratory population can be used in future work throughout the year to obtain results that are consistent with

the dynamics of the natural population. Results may be obtained quicker, leading to a smaller length of time before the population dynamics of the Western Spruce budworm are understood and effective management programs implemented.

ACKNOWLEDGEMENTS

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FIGURE CAPTIONS

FIGURE 1. Distribution of the number of WSBW eggs in F_1 egg masses greater than three square millimeters. The solid line indicates a normal distribution.

FIGURE 2. Distribution of the number of WSBW larvae hatched from F_1 egg masses greater than three square millimeters. The solid line indicates a normal distribution.

FIGURE 3. Hatch success of wild and lab-reared F_1 eggs on Douglas-fir needles. The proportion of eggs between wild and lab bags for each group is non-significant ($p > 0.5$).

FIGURE 4. Hatch success of F_1 eggs from lab-reared larvae placed either on early (young) or late (mature) Douglas-fir foliage. The proportion of eggs between early and late bags for each group is non-significant ($p > 0.3$).

FIGURE 5. Pupal survival rates between sexes and between treatments. Sample sizes are given above the bars. A Chi-square test revealed non-significance among groups ($p > 0.1$).

FIGURE 6. Pupal mass by sex and treatment. Female pupae are significantly heavier than male pupae ($t_6 = 145.33$, $p < 0.0001$). Wild pupae are heavier than lab pupae and lab pupae are heavier than late lab pupae ($p < 0.05$ for all comparisons), but the

difference in mass between groups ranges only from 11-16 percent.

FIGURE 7. Pupal mass in relation to tree age. Female pupal mass does not seem to be affected by tree age ($r = 0.212$, $p > 0.05$). Male pupal mass may be affected by tree age ($r = 0.453$, $p < 0.01$). However, there is considerable variation around the regression line, suggesting that tree age may not be as important as other extrinsic factors.

Table 1. One way ANOVA comparing the mean number of larvae emerged from F1 egg masses between wild and lab-reared Western Spruce budworm.

Source of Variation	Sum of Squares	d.f.	Mean Square	F	p-value
Between groups	19.652	1	19.65218	0.125	0.7278
Within groups	92,133.407	585	157.49300		
Total	92,153.060	586			

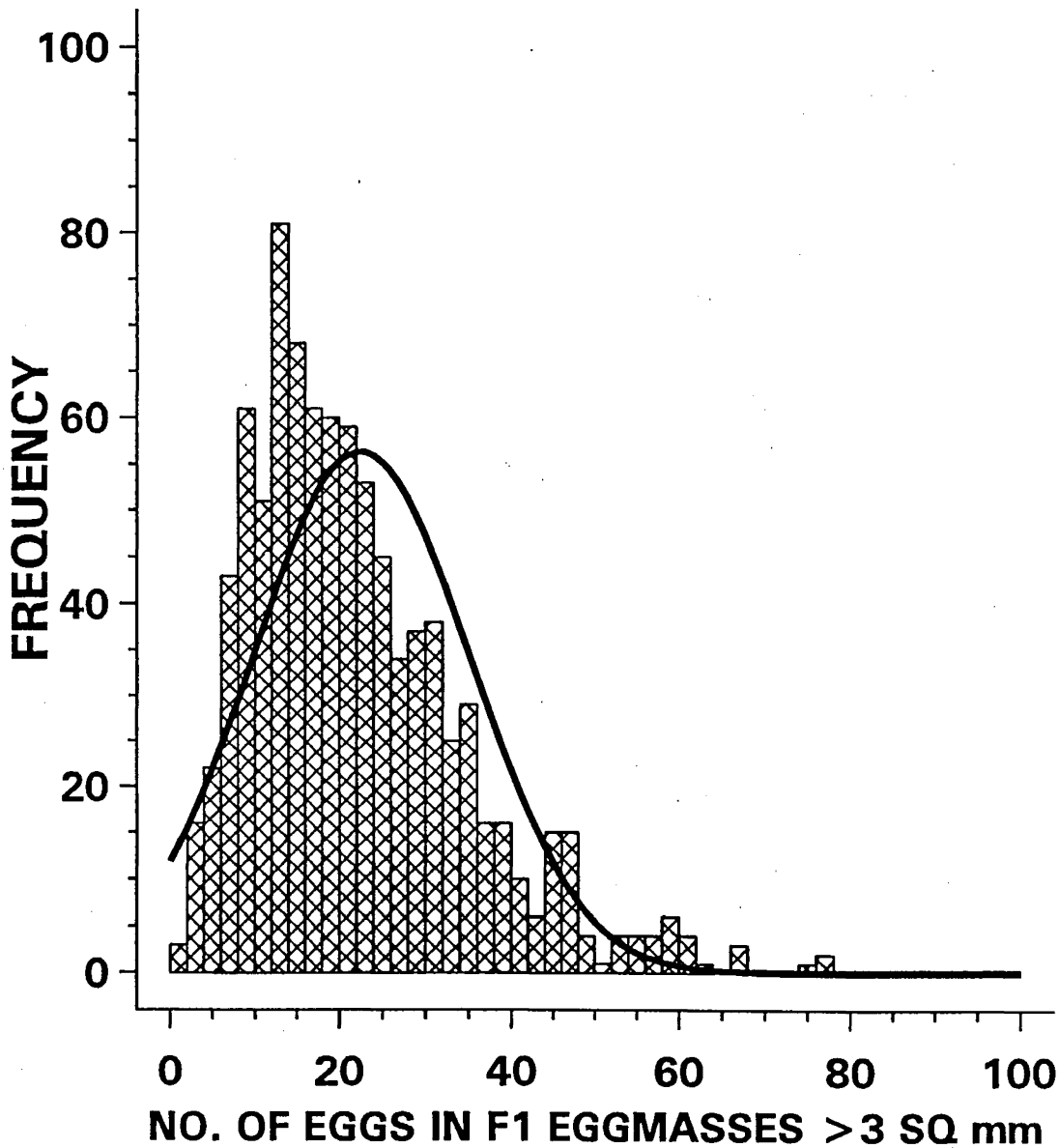
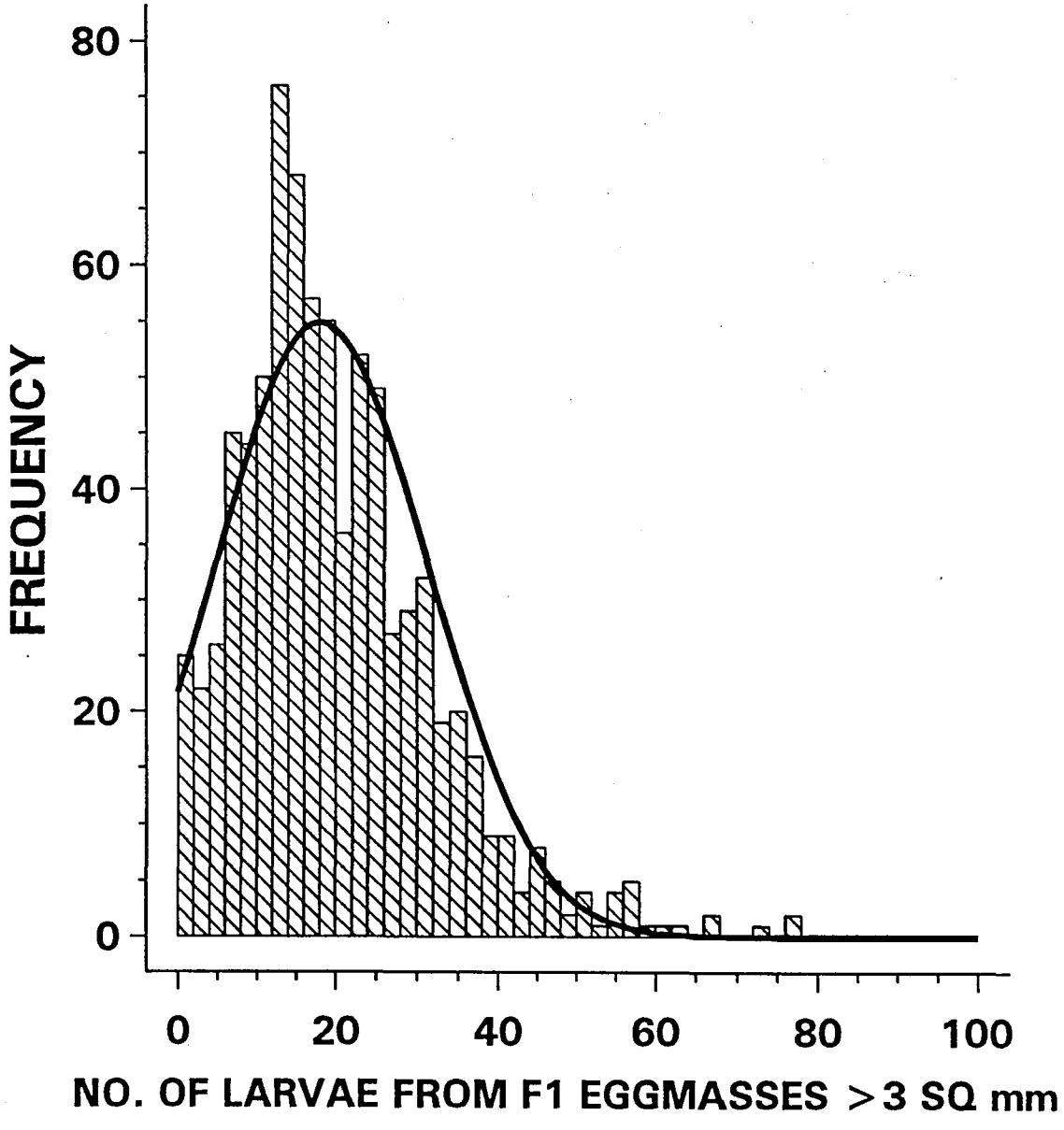

100
80
60
40
20
0
FREQUENCY
0
20
40
60
80
100
NO. OF EGGS IN F1 EGGMASSES >3 SQ mm

Fig. 1


80
60
40
20
0
FREQUENCY
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20
40
60
80
100
NO. OF LARVAE FROM F1 EGGMASSES >3 SQ mm

Fig. 2

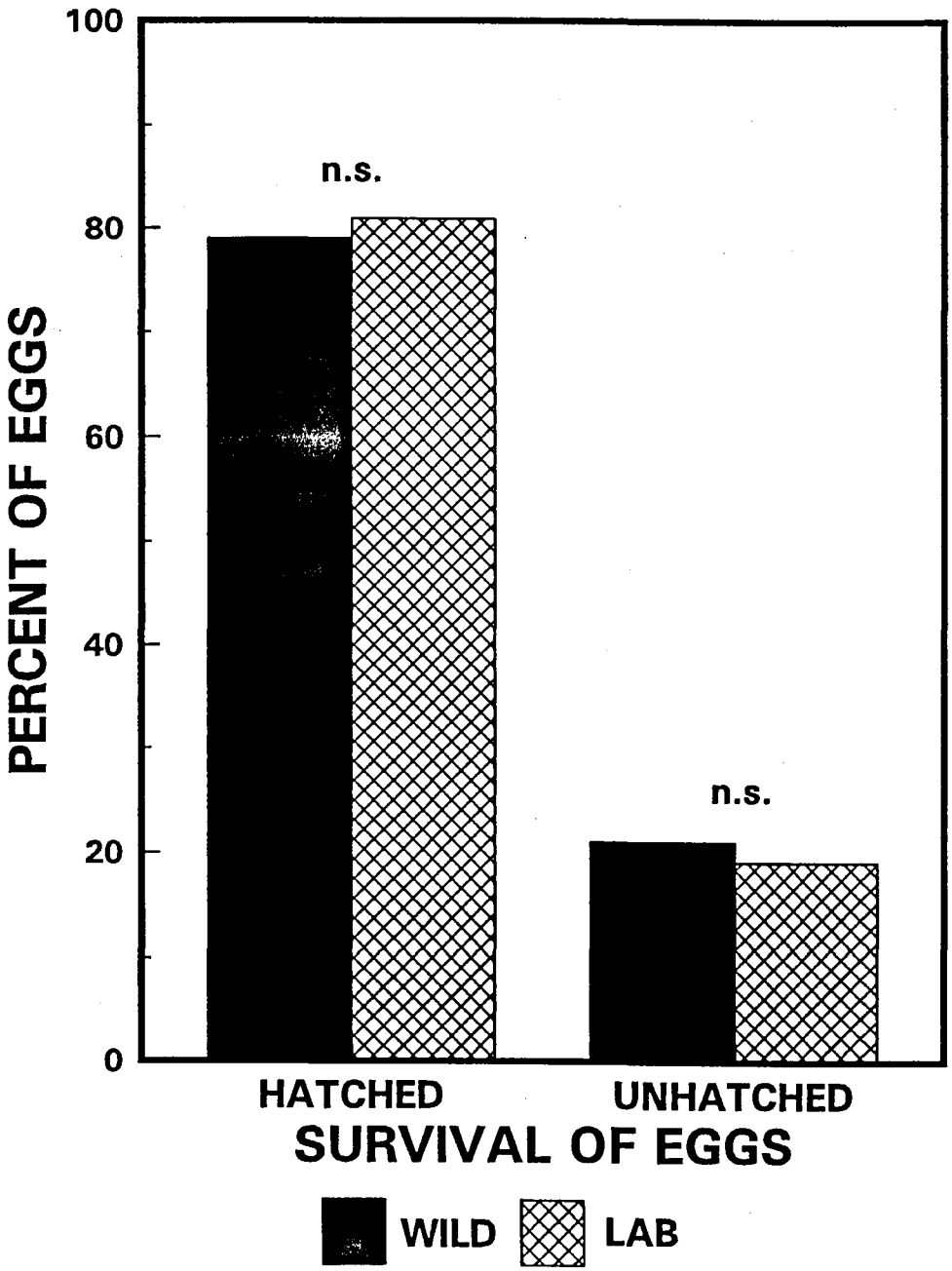

100
80
60
40
20
0
PERCENT OF EGGS
n.s.
n.s.
HATCHED
UNHATCHED
SURVIVAL OF EGGS
WILD
LAB

Fig. 3

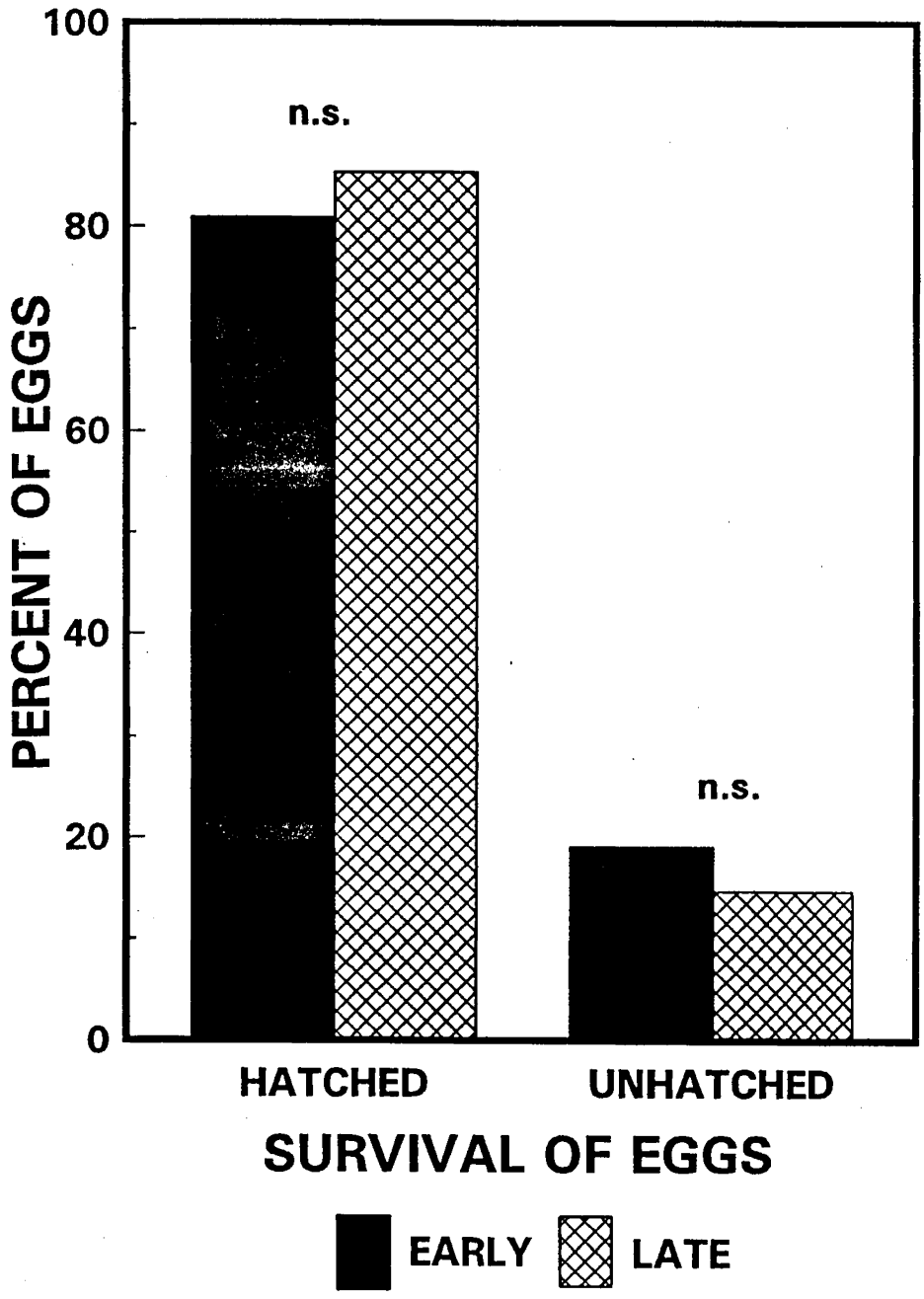
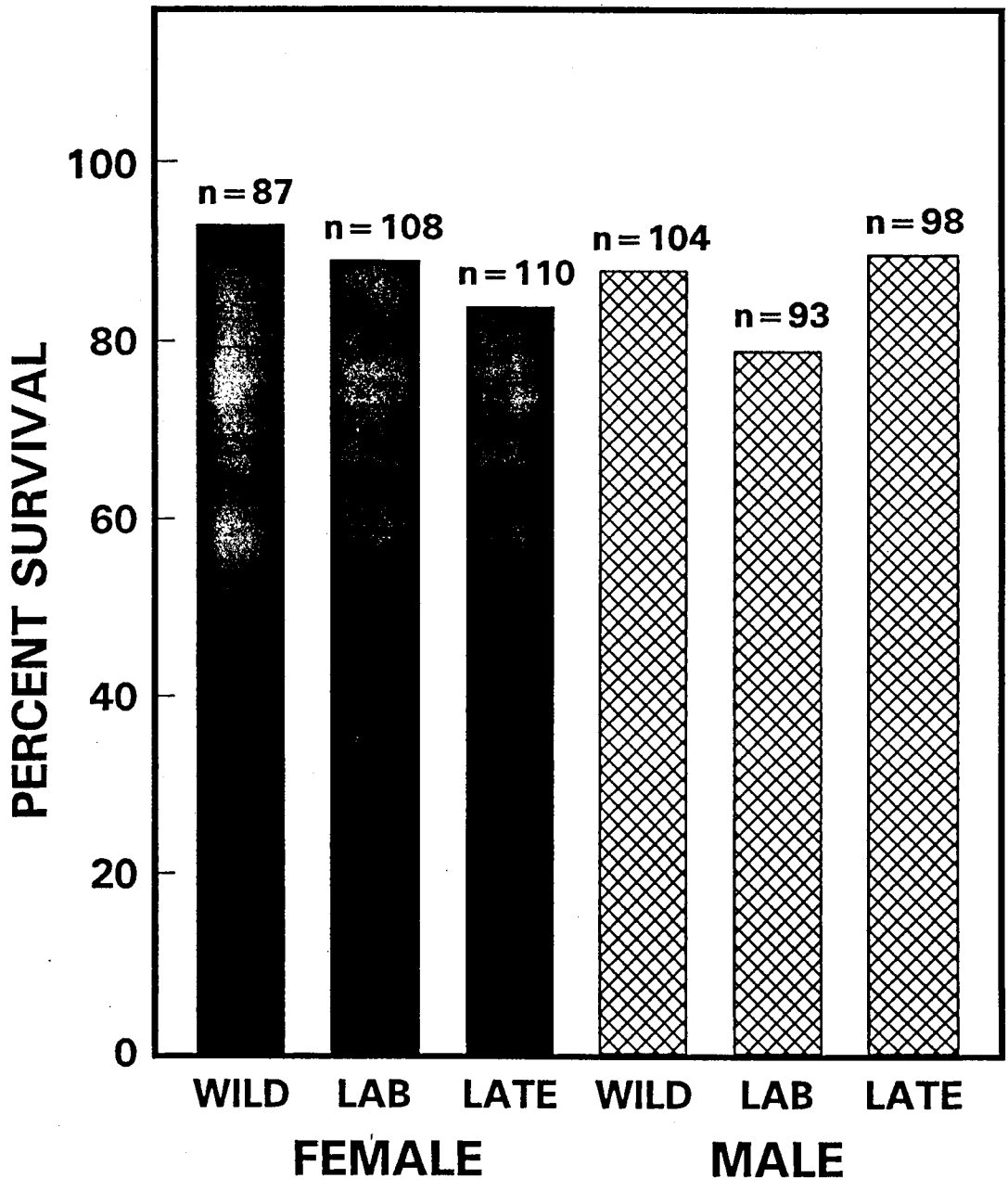

100
80
60
40
20
0
PERCENT OF EGGS
n.s.
n.s.
HATCHED
UNHATCHED
SURVIVAL OF EGGS
EARLY
LATE

Fig. 4


PERCENT SURVIVAL
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80
60
40
20
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n=87
n=108
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n=93
n=98
WILD
LAB
LATE
WILD
LAB
LATE
FEMALE
MALE

Fig. 5

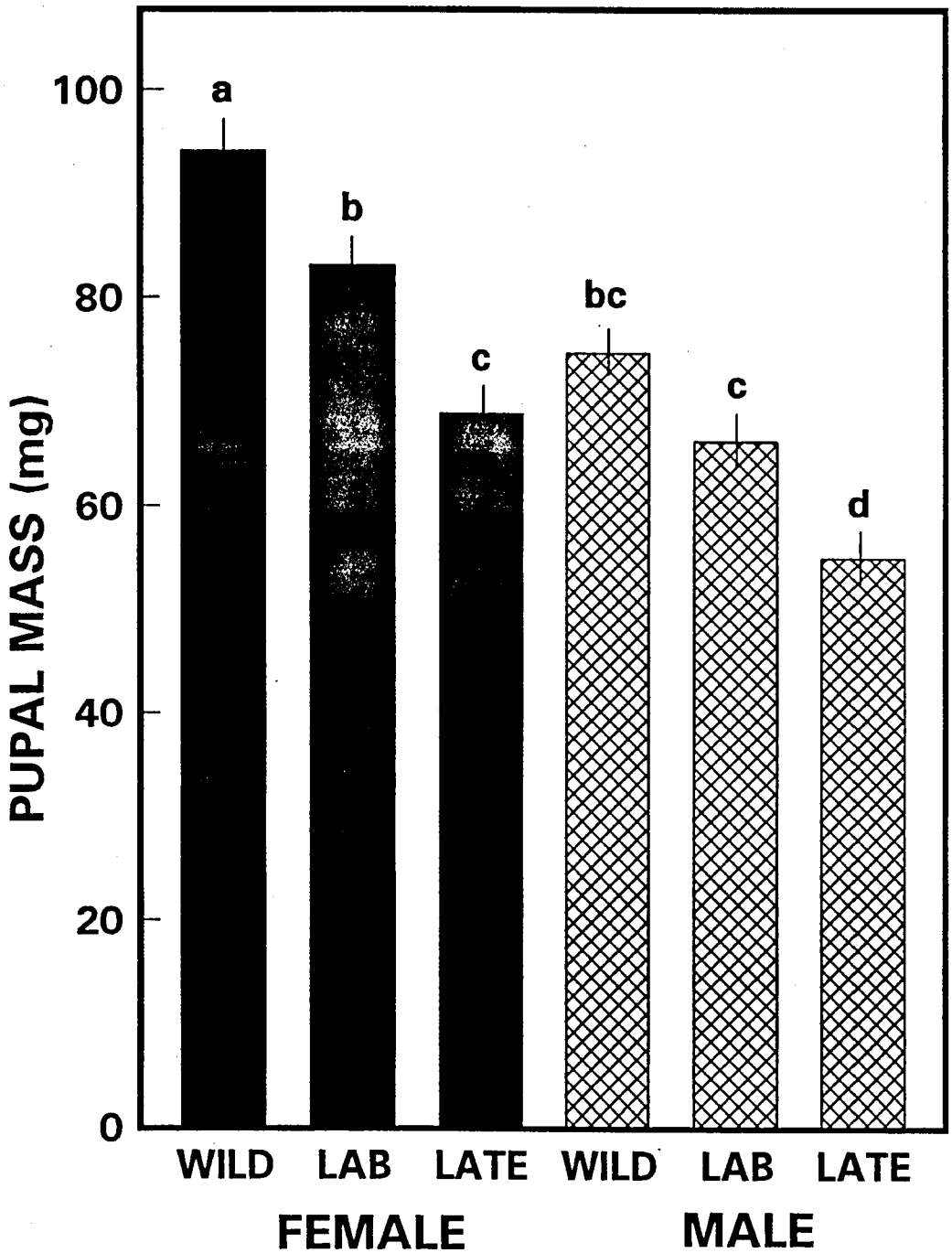
100
80
60
40
20
0
PUPAL MASS (mg)
a
b
c
bc
c
d
WILD
LAB
LATE
WILD
LAB
LATE
FEMALE
MALE

Fig. 6

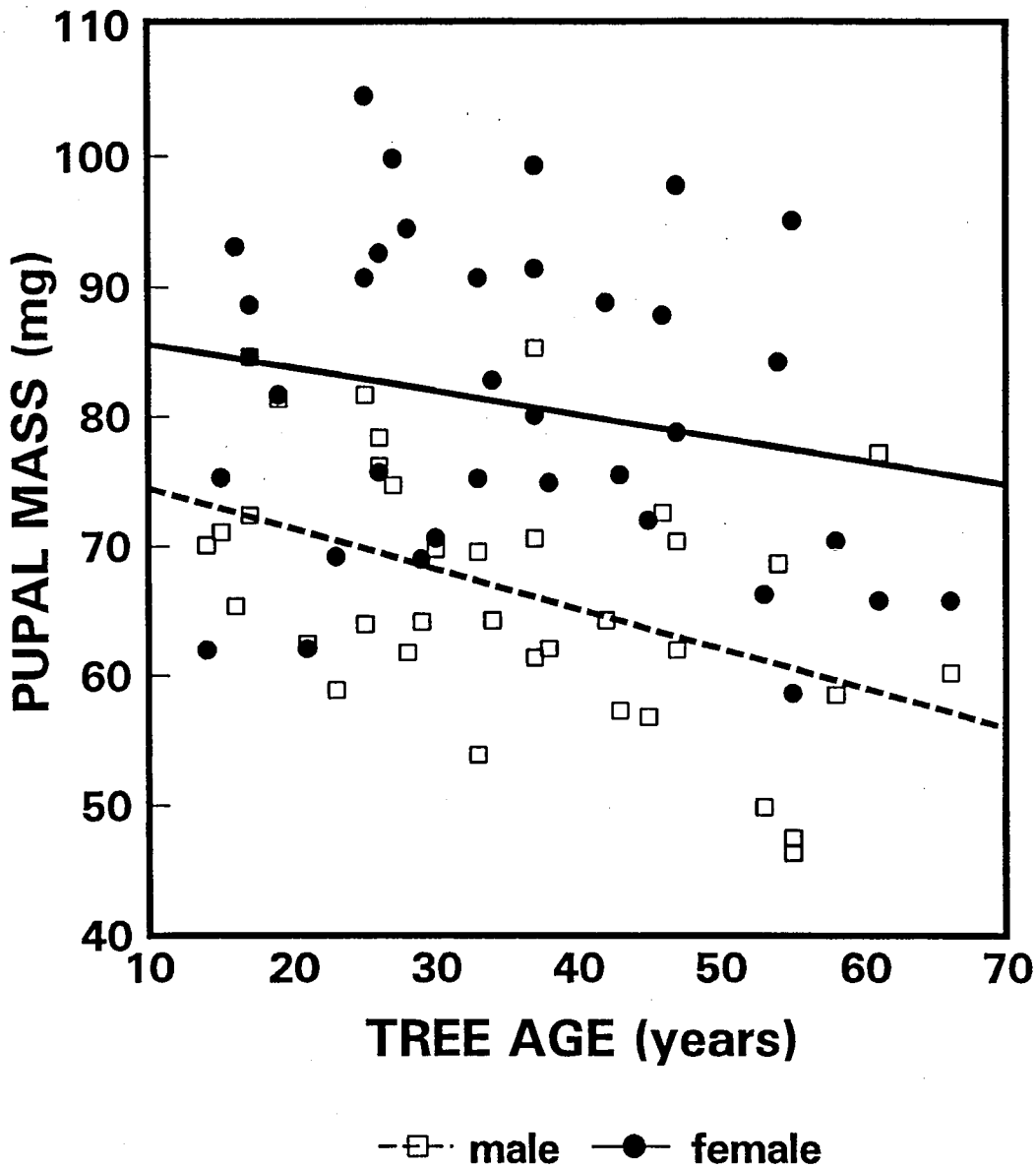
110
100
90
80
70
60
50
40
PUPAL MASS (mg)
10
20
30
40
50
60
70
TREE AGE (years)
male
female

Fig. 7